

Update on Signaling

Jasmonate, Genes, and Fragrant Signals¹

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Although first recognized for its growth-inhibiting activity about 20 years ago, JA² and its fragrant methyl ester MeJA (referred to here collectively as jasmonate) are receiving renewed interest as potentially important signaling molecules in plants. This is because jasmonate markedly increases the expression of specific plant genes, some of which are wound responsive. Similarities with fatty acid-derived stress signaling molecules in animals (1) make jasmonate of general biological interest.

IS JASMONATE A PLANT HORMONE?

Jasmonate has many of the general characteristics of a hormone, or plant growth regulator, which is defined as an endogenous plant substance that acts at low concentration to affect physiological processes (3). However, hormone status has historically been conferred by consensus over time, rather than by definition. Davies (3) appropriately contends that whether a compound is classified as a hormone is irrelevant. What is important is that we identify the endogenous substances that control plant development, gene expression, and response to the environment and determine how they act.

MeJA is a constituent of the fragrance from several flowers (e.g. jasmine) and fruits. This volatile oil is used by the perfume industry and consequently has been synthesized in relatively large quantities. In plants, JA [3-oxo-2-(2'-*cis*-pentenyl)-cyclopentane-1-acetic acid] is synthesized from α -linolenic acid by a lipoxygenase-mediated oxygenation, followed by additional modifications (19). The potentially important role of lipoxygenase in controlling JA synthesis has increased interest in its study as well.

JA and/or its methyl ester probably occur in most organs of most plant species (14). The quantities estimated by various methods are typical of other plant hormones, ranging from about 10 ng to as much 3 μ g/g fresh weight in different tissues and species. The acid seems to be the more prevalent form; the methyl ester is usually more active when applied exogenously (4), although there are exceptions (20). The higher activity of MeJA may be due to the fact that it is more volatile and not ionized, possibly enhancing its incorporation into plant tissues.

Four stereoisomers of jasmonate are possible. Evaluating the efficacy of jasmonate is complicated by the fact that

(–)jasmonate is easily epimerized to the (+)isomer, which apparently has lower biological activity (19). Commercial preparations contain mostly (+)MeJA. Consequently, the potency of jasmonate may be underestimated and results are difficult to compare among laboratories. The situation is further complicated by the presence of several derivatives and closely related compounds in plants, some of which have similar activities.

JASMONATE ELICITS A VARIETY OF PLANT RESPONSES

Among the many observed effects of exogenously applied jasmonate are the promotion of senescence, petiole abscission, root formation, tendril coiling (4), ethylene synthesis, and β -carotene synthesis. On the other hand, jasmonate has been reported to inhibit seed germination, callus growth, root growth, Chl production, and pollen germination (1, 15, 19, and references therein).

Not surprisingly, some of the reported effects are contradictory among species, and we should expect that not all are hormonal responses. For example, inhibition of growth, promotion of senescence, and stomatal closure were recently suggested to result from the use of toxic amounts of JA or MeJA (1, 10). Furthermore, jasmonate is usually more abundant in young organs, which is inconsistent with its suggested role in senescence.

JASMONATE INDUCES GENE EXPRESSION

The expression of a number of genes is altered in response to jasmonate. An analysis of 30 plant species, including both monocots and dicots, found multiple jasmonate-induced proteins in all but 4 species (8). Proteins of known function that are induced by JA or MeJA include the VSPs of soybean (17), the wound-induced proteinase inhibitors of tomato and potato (6), and seed storage proteins and oil body membrane proteins (oleosins) in developing *Brassica napus* embryos (20). The genes that encode these proteins are induced by other signals as well. They are developmentally regulated and the VSP and proteinase inhibitor genes respond to wounding (6, 13). The proteinase inhibitor genes and some genes for embryo proteins are also induced by ABA.

MeJA joins ethylene as one of the few endogenous plant compounds known to elicit plant responses as a gas. Leaf proteinase inhibitors are induced by atmospheric MeJA (6) at concentrations estimated to be 40 to 80 nM or less (4). Atmospheric MeJA also induces soybean VSPs and stimulates

¹ This is paper No. 9872, Journal Series, Nebraska Agricultural Research Division

² Abbreviations: JA, jasmonic acid; MeJA, methyl jasmonate; VSP, vegetative storage protein.

tendrils in *Bryonia dioica*, the latter a reaction triggered by mechanical stimulation in nature (4). Strikingly, sagebrush (*Artemisia tridentata*) appears to release MeJA to the air in sufficient quantity to induce proteinase inhibitors in plants incubated in the same chamber. On the other hand, JA is only effective when applied directly to leaves, probably because it is less volatile than MeJA (5). It remains to be seen whether volatile MeJA is an effective natural signal between plants. Air currents would probably prevent accumulation of sufficient concentrations of jasmonate to elicit a response in most situations.

ENDOGENOUS JASMONATE MAY BE A SYSTEMIC SIGNAL

Evidence for the involvement of endogenous jasmonate in the control of plant gene expression is still circumstantial. In general, the amount of jasmonate is highest in young organs (12, 14), which correlates with the developmental pattern of expression for the VSP genes in soybean. The concentration of JA and/or MeJA appears to be sufficient for a physiological role.

The soybean VSP genes exhibit cell-specific expression, primarily in the vascular bundle sheath and associated tissues (11). Interestingly, MeJA was reported to be at highest concentration in vascular regions of soybean pericarp tissue (15), where expression of the VSP genes is also greatest (11). On the other hand, exogenous application of MeJA induces expression of the VSP genes and protein accumulation in all leaf cell types. One interpretation of this result is that leaf cells differ in the amount of jasmonate they contain, or in their sensitivity to jasmonate, which contributes to the cell-specific expression of the VSP genes.

Other evidence also implicates endogenous jasmonate in gene regulation. Wound induction of the VSP genes is blocked by pretreatment with lipoxygenase inhibitors (18), whereas exogenous MeJA remains fully effective in VSP gene induction. In another approach, precursors of JA were shown to induce tomato proteinase inhibitors, but closely related compounds that are not JA precursors were ineffective (7). Although not definitive, these results are consistent with the idea that wound signaling involves *de novo* synthesis of jasmonate, which may be controlled by the availability of free linolenic acid substrate for JA biosynthesis (7, 19). Phospholipases may control the release of membrane fatty acids in this scenario (1).

Wounding induces a systemic response in untreated leaves of many plants, including the induction of soybean VSP (12, 17) and protease inhibitors (5). Jasmonate also induces protease inhibitors in distant untreated leaves, and assimilation of MeJA through soybean petioles is an effective way to induce VSP gene expression in leaf explants (13, 18). However, it has not been demonstrated that jasmonate is the transported signal. Whether jasmonate is synthesized and mobilized to distant sites in response to wounding also has not been reported. Other systemic signals (16) or entirely different signaling mechanisms are also possible.

RELATIONSHIP OF JASMONATE TO OTHER GENE REGULATORS

There are similarities as well as differences in the structure, physical properties, and activity of ABA and jasmonate. Both induce the proteinase inhibitors and *Brassica* seed storage proteins (20), but only jasmonate induces the soybean VSP genes (1). An understanding of the role of interactions between jasmonate, ABA, and other plant hormones in regulating plant development and metabolism will require considerably more investigation. Soluble sugars and nitrogen also affect the induction of VSP genes by MeJA (12, 18). The diversity of stimuli that influence these genes suggests that their regulation is complex.

Farmer and Ryan (7) recently outlined a model for wound induction of proteinase inhibitor genes, incorporating much of what is known about their regulation. Wounding is proposed to activate systemin, perhaps by releasing this potent 18-amino acid peptide from an inactive propeptide. Systemin could serve as a systemic signal that releases linolenic acid from membranes after binding to a plasma membrane receptor. Jasmonate synthesized from linolenic acid in turn might activate genes, possibly through another receptor. Presumably there are *cis* promoter sequence elements and their respective nuclear *trans*-acting factors that facilitate expression of the jasmonate-responsive genes. Figure 1 outlines a possible role for jasmonate in developmental and wound-induced expression of the soybean VSP genes.

JASMONATE HAS BIOLOGICAL ACTIVITY IN OTHER ORGANISMS

Plants are not the only organisms that respond to MeJA. It is an active component of the female-attracting pheromone released by male oriental fruit moths (2) and may be synthesized by the moths or ingested with the fruit they eat. Other volatile plant substances, including ethylene and some responsible for floral fragrance, are powerful attractants or stimulators of specific insect responses. Based on the important role of the related animal eicosanoids in signaling, it is perhaps not surprising that jasmonate has biological activity in other organisms.

Jasmonate is also found in at least one plant pathogenic fungus, and α -linolenic acid is present in several fungi. Oxidation products of lipoxygenase influence vegetative *versus* reproductive growth in some fungi (9), and it is interesting that some lipoxygenase inhibitors are antifungal agents. Jasmonate and related molecules may be important signaling molecules in fungi, but a definitive understanding of their function awaits further study.

Jasmonate may also effect signaling between different organisms that are in close association. It is pertinent to investigate whether MeJA or related compounds are released by microorganisms in sufficient quantity to signal localized plant defense responses. Conversely, plants might influence microorganism growth and development via endogenous jasmonate.

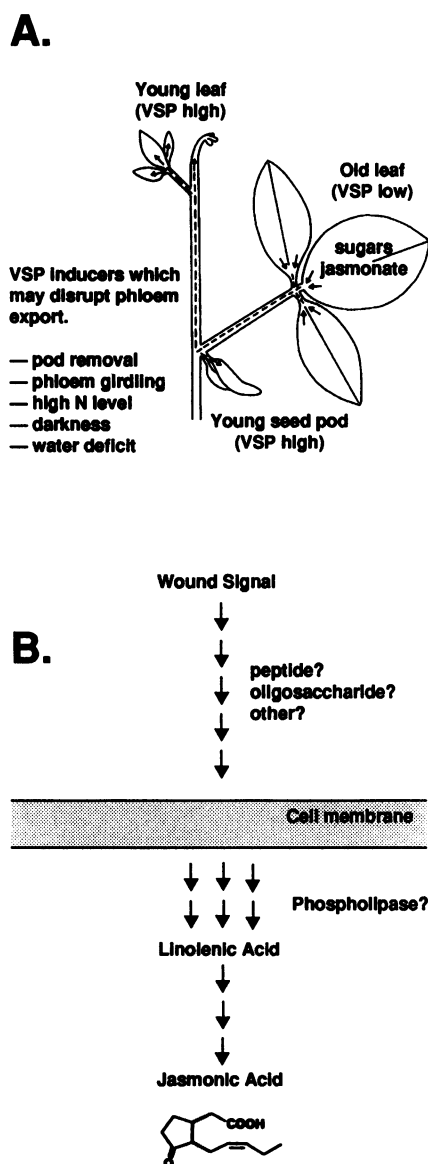


Figure 1. Model for the role of jasmonate and soluble sugars in soybean VSP gene expression. A, Accumulation of jasmonate and sugars exported from older (source) leaves to developing organs (sinks) may stimulate VSP genes in the latter. Disrupting export may increase jasmonate and soluble carbohydrate concentration in older leaves and stimulate VSP gene expression. B, Wound induction of jasmonate synthesis following release of membrane fatty acids.

CONCLUSIONS

The current intense effort to identify endogenous signals that regulate gene expression has generated considerable interest in the mechanism of jasmonate action in plants. Although substantial progress has been made recently, significant gaps in our understanding remain, particularly regarding the putative role of receptors and phospholipases, the identity of the systemic wound signal(s), and the gene regulatory elements and DNA binding factors that confer jasmonate inducibility to certain genes. The intracellular lo-

cation of jasmonate and regulation of its biosynthesis are also poorly understood. The isolation of mutants defective in jasmonate biosynthesis or in their response to jasmonate would lead to a better understanding of the role of this compound in plants, and possibly to the isolation of genes involved in jasmonate signal transduction. The powerful genetic, molecular, and biochemical techniques currently available should allow rapid progress toward understanding the extent to which plants control development, respond to stress, and direct other processes with a "fragrant signal."

ACKNOWLEDGMENTS

Appreciation is extended to Drs. J.E. Mullet and C.A. Ryan for providing copies of manuscripts that were in press.

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